



Growth and population dynamic model of the reef coral *Fungia granulosa* Klunzinger, 1879 at Eilat, northern Red Sea

Nanette E. Chadwick-Furman^{a,b,*}, Stefano Goffredo^c, Yossi Loya^d

^aInteruniversity Institute for Marine Science, P.O. Box 469, Eilat, Israel

^bFaculty of Life Sciences, Bar Ilan University, Ramat Gan, Israel

^cDepartment of Evolutionary and Experimental Biology, University of Bologna, via Selmi 3, I-40126 Bologna, Italy

^dDepartment of Zoology, The George S. Wise Faculty of Life Sciences, and the Porter Super-Center for Ecological and Environmental Studies, Tel Aviv University, Tel Aviv, Israel

Received 18 August 1999; received in revised form 10 February 2000; accepted 9 March 2000

Abstract

The lack of population dynamic information for most species of stony corals is due in part to their complicated life histories that may include fission, fusion and partial mortality of colonies, leading to an uncoupling of coral age and size. However, some reef-building corals may produce compact upright or free-living individuals in which the above processes rarely occur, or are clearly detectable. In some of these corals, individual age may be determined from size, and standard growth and population dynamic models may be applied to gain an accurate picture of their life history. We measured long-term growth rates (up to 2.5 years) of individuals of the free-living mushroom coral *Fungia granulosa* Klunzinger, 1879 at Eilat, northern Red Sea, and determined the size structure of a population on the shallow reef slope. We then applied growth and population models to the data to obtain estimates of coral age, mortality rate, and life expectancy in members of this species. In the field, few *F. granulosa* polyps suffered partial mortality of > 10% of their tissues. Thus, the majority of polyps grew isometrically and determinately, virtually ceasing growth by about 30–40 years of age. Coral ages as revealed by skeletal growth rings were similar to those estimated from a growth curve based on field data. The frequency of individuals in each age class on the reef slope decreased exponentially with coral age, indicating high mortality rates when corals were young. The maximum coral age observed in the field population (31 years) was similar to that estimated by application of a population dynamic model (30 years). Calculated rates of growth, mortality and life expectancy for *F. granulosa* were within the range of those known for other stony corals. Our results reveal a young, dynamic population of this species on Eilat reefs, with high turnover rates and short lifespans. Such information is important for understanding

*Corresponding author. Tel.: +972-7-636-0101; fax: +972-7-637-4329.

E-mail address: furman@mail.biu.ac.il (N.E. Chadwick-Furman)

recovery of coral reefs from disturbances, and for application to the management of commercially exploited coral populations. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Fungiidae; Growth model; Mushroom coral; Population ecology; Red Sea; Reef management; Scleractinia

1. Introduction

Processes of population turnover among stony reef-building corals are important in that they influence how rapidly and to what extent coral reefs recover from disturbances (Connell, 1973). Patterns of larval survival, juvenile recruitment, somatic growth, sexual reproduction and mortality vary widely among species of corals, and play a decisive role in species succession on developing reefs (Grigg and Maragos, 1974; Hughes and Jackson, 1985). Some scleractinians, such as species of the branching corals *Stylophora* and *Pocillopora*, have been classified as r-strategists in that they produce a large number of propagules over a long season each year, grow rapidly, and are among the first to colonise newly created space on reefs (Grigg and Maragos, 1974; Loya, 1976a,b; Connell et al., 1997). Others, in particular those with massive hemispherical growth forms such as some species of *Porites* and *Platygyra*, may be K-strategists in that they reproduce only during a short period each year and grow slowly (Babcock, 1991; Shlesinger and Loya, 1991), and thus may take several years to colonize new substrata, but once established are able to dominate reefs via effective defense of living space (Grigg and Maragos, 1974). Thus, the life history characteristics of each coral species may explain in large part the observed variation in coral community structure between patches with different disturbance histories on shallow reefs.

The current lack of basic population dynamic information for most stony corals is due in part to a distortion of the relationship between colony size, age and genetic origin, because many colonies may experience fission, fusion, or partial mortality (Hughes and Jackson, 1985; Babcock, 1991). Thus, studies on foliaceous and encrusting corals have relied on long-term observations of individual colonies in order to determine their history and origins, and have used size-based rather than age-based models of population dynamics (Hughes, 1984; Hughes and Jackson (1985), but see Babcock (1991) for a combination of models). However, some corals on reefs grow in distinct forms that rarely undergo fission or fuse, and in which partial mortality is clearly detectable by distortions of the regular growth form. These include stony corals that build compact branching colonies, such as *Pocillopora* (Grigg, 1984; Ross, 1984) and *Stylophora* (Loya, 1976a), some with massive hemispherical growth forms such as *Platygyra* and *Goniastrea* (Babcock, 1991), and free-living corals such as *Fungia* (Chadwick and Loya, 1990), *Manicina* (Johnson, 1992) and *Siderastrea* (Lewis, 1989). In some of these corals, individuals may be aged reliably, thus standard age-based growth and population dynamic models may be applied to understand their demography.

The population dynamic model developed for fisheries by Beverton and Holt has been applied successfully to many marine invertebrates (reviewed by Clasing et al. (1994)),

including the scleractinian corals *Pocillopora verrucosa* (Grigg, 1984; Ross, 1984) and *Balanophyllia europaea* (Goffredo, 1999). This model also has been proposed for use in managing exploited populations of stony reef corals in the Philippines (Ross, 1984). The Beverton Holt model characterises the population dynamics of a given species based on the size frequency distribution of individuals in the field, individual growth rates, and the relationship between individual mass and length. The most important constraint of this model is the assumption that a population is in steady state, in other words that no major disturbance has recently altered population size structure. For species of short-lived corals, or those in relatively deep or stable environments, this may not be a serious limitation (Fadlallah, 1983; Grigg, 1984; Ross, 1984; Mistri, 1995). This is a cohort-based model, in which a cohort of recruits is estimated to gain biomass until an age–size point at which losses to the cohort due to mortality overtake gains in biomass due to individual growth. After this point, as the cohort ages, its biomass declines to zero, as very few individuals of large size remain in the population. The individual size that corresponds to the age at peak cohort biomass is the minimum size of individuals that can be removed from the population in a sustainable manner, without decimating it.

In order to apply this population model to corals, growth rate data must be converted to age–size relationships. In corals that grow indeterminately, if processes of partial mortality or fragmentation do not interfere, age is a linear function of individual length (Loya, 1976a; Grigg, 1984; Ross, 1984; Babcock, 1991). However, in reef-building corals with size-dependent growth, age–size relationships must be estimated using a growth curve, because growth rate decreases as the individuals age. The von Bertalanffy growth curve (von Bertalanffy, 1938) models size-dependent growth, and has been applied widely to estimate age–size relationships in various invertebrates (reviewed by Stokes (1996)). This model curve also has been used to describe growth patterns in cnidarians, including some gorgonians (Grigg, 1974; Mistri and Ceccherelli, 1993, 1994) and solitary scleractinians (Gerrodette, 1979; Bablet, 1985; Goffredo, 1995).

Population dynamic and growth models are important tools for understanding patterns of turnover and change among stony corals on reefs. Such models also are increasingly needed to manage the sustainable harvest of reef corals for the ornamental aquarium industry (Ross, 1984), and to assess the health of exploited reefs (Bak and Meesters, 1998). Until the late 1980s, coral reefs in the Philippines produced most of the world's stony corals for ornamental use (Ross, 1984). More recently, an increasing proportion of stony corals are being collected from reefs in Indonesia (Bentley, 1998). Harvesting of corals from reef populations resulted in imports of scleractinians to the United States alone averaging about \$1 million annually during 1975 to 1980 (Grigg, 1984), and continuing at about 1 million pieces imported per year in the 1990s (Bentley, 1998). Coral resources may be managed successfully by the application of population models to determine a maximum sustainable yield for each species, based on a minimum size or age for collection (Grigg, 1984).

Most members of the scleractinian family Fungiidae (mushroom corals) form unique free-living polyps on coral reefs, and are particularly vulnerable to overexploitation. In many mushroom corals, small attached polyps actively dissolve the skeleton near the polyp base, and become detached, free-living individuals (reviewed by Hoeksema (1989) and Yamashiro (1992)). Due to their mobility, many mushroom corals move off

the reef and colonize the sandy base, where they may serve as nuclei for the formation of new patch reefs (Chadwick-Furman and Loya (1992) and references therein). Thus, mushroom corals are initiators of reef growth, and sometimes are major components of reef flats (Kramarsky-Winter and Loya, 1998) and slopes (Goffredo and Chadwick-Furman, 2000). Because they also reproduce asexually, the members of some species recover rapidly after disturbances (Loya, 1975), and may even build large patch reefs consisting only of mushroom corals (Littler et al., 1997).

Mushroom corals also are one of the major components of international trade in ornamental corals (Bentley, 1998). They constituted > 60% of the coral fishery in the Philippines in the 1980s, where they far outnumbered all other types of stony corals collected (Ross, 1984). Even though the coral curio industry has shifted to Indonesian reefs, mushroom corals remain in high commercial demand (Bentley, 1998) due to their large polyp size, ease of collection, and popularity among consumers. Thus, the development of accurate models of population turnover and growth in fungiid corals is important in order to understand basic reef processes, and for application to the management of exploited reef coral populations. Finally, fungiids may serve as an ideal group for the application of population dynamic models, because in many species, age and size are directly related. In the free-living polyps of many mushroom corals, shape is constant over the lifespan, fission and fusion are rare, and evidence of partial mortality is clearly visible on the disk due to its shape (Hoeksema, 1989; Chadwick and Loya, 1990).

Individuals of the mushroom coral *Fungia granulosa* Klunzinger, 1879 are a common component of the stony coral assemblage on reefs at Eilat, northern Red Sea (Kramarsky-Winter and Loya, 1998; Goffredo and Chadwick-Furman, 2000). Members of this species form dioecious polyps that spawn gametes during July to August each year (Kramarsky-Winter and Loya, 1998). The duration of the larval phase is unknown, but polyps appear to recruit at 2–9 m depth at Eilat, and then to detach actively and migrate down to at least 33 m depth as adults (Goffredo and Chadwick-Furman, 2000). The goals of the present study were to determine patterns of individual shape and size, long-term growth, and field population structure in *F. granulosa*, and then to apply population and growth models (see above) to estimate rates of mortality, population turnover and lifespan. We also compare here the life history characteristics of this species with those known for other scleractinians, and discuss the application of population models to the management of commercially exploited stony corals on tropical reefs.

2. Materials and methods

This study was conducted on reefs adjacent to the Interuniversity Institute for Marine Science (IUI) at Eilat, northern Red Sea. Growth rates of 131 individuals of *Fungia granulosa* were measured at 5–7 m depth on the reef slope during September 1992–March 1995. This depth was chosen because it contains many individuals of this species (Goffredo and Chadwick-Furman, 2000). Each coral was measured for 0.5–2.5 years. The period of measurement varied between individuals, because corals that died were

replaced by others of similar size during the study. The measured polyps were contained in wide, flat baskets (30 cm long \times 20 cm wide \times 4 cm high) on the reef slope in order to prevent their dispersal and loss during the growth study. The bottom of each basket was attached to a cement brick for stability, and \sim 10 polyps spanning the size range for *F. granulosa* were placed inside. The baskets were open on top, in order to simulate a small natural depression in the reef, and to minimize any artifacts of altered water flow, light, or predation patterns on the corals. The polyps in each basket were individually recognisable due to their sizes and individual markings (color pattern, polyp outline, after Chadwick-Furman and Loya (1992)). Each 3 months during the study, all polyps were examined in situ, and their length (along the mouth axis), width (perpendicular to the mouth axis, after Abe (1940) and Bablet (1985)), and polyp condition (% tissue mortality) were recorded. We include here data only for polyps that had $<$ 10% tissue mortality throughout the study, thus the growth rates reported here represent maximal values for polyps in each size class.

The skeletons of polyps that died naturally during the study ($N = 35$) were removed from the sea, dried at 400°C for 24 h, and their length and dry skeletal mass obtained. We also counted circular rings that were externally visible on the aboral surface of each skeleton (Fig. 1). These rings have been shown to correspond to annual growth in the congener *F. actiniformis* (Abe, 1940). Growth rings were counted only on relatively small corals ($<$ 60 mm length), because on larger individuals they were too close together to distinguish externally.

The population size structure of *F. granulosa* was determined by examining polyps on the Japanese Gardens fringing reef, \sim 500 m north of the IUI. This reef area was chosen for population sampling because it is a well-developed fringing reef with many mushroom corals (Goffredo and Chadwick-Furman, 2000), its coral community structure has been well-studied (reviewed by Loya, 1990), and it occurs inside a fenced, inaccessible portion of the Coral Beach Nature Reserve of Eilat, thus being largely protected from human impacts to coral populations on the reef slope. A belt transect (1 \times 25 m) was deployed parallel to shore on the reef slope at each of five depths: 2, 3, 6, 9, and 12 m, thus encompassing the depth range of most of the *F. granulosa* population on the Japanese Gardens reef (Goffredo and Chadwick-Furman, 2000; but see Kramarsky-Winter and Loya (1998) for a different depth range on other reefs). Within each transect, all *F. granulosa* polyps were examined, and their length, width (as defined above), and attached versus free-living status were recorded.

We then used mathematical models to describe patterns of growth and population dynamics for *F. granulosa* at Eilat, by applying the von Bertalanffy growth function and the Beverton Holt population dynamics model (see above).

3. Results

As expected for a disc-shaped coral, mass increased exponentially with length in individuals of *Fungia granulosa* (Fig. 2A). Width varied linearly with length (Fig. 2B), and the width:length ratio of polyps remained constant throughout the lifespan (Fig. 2C), indicating that the corals did not change shape as they aged, and thus that growth was

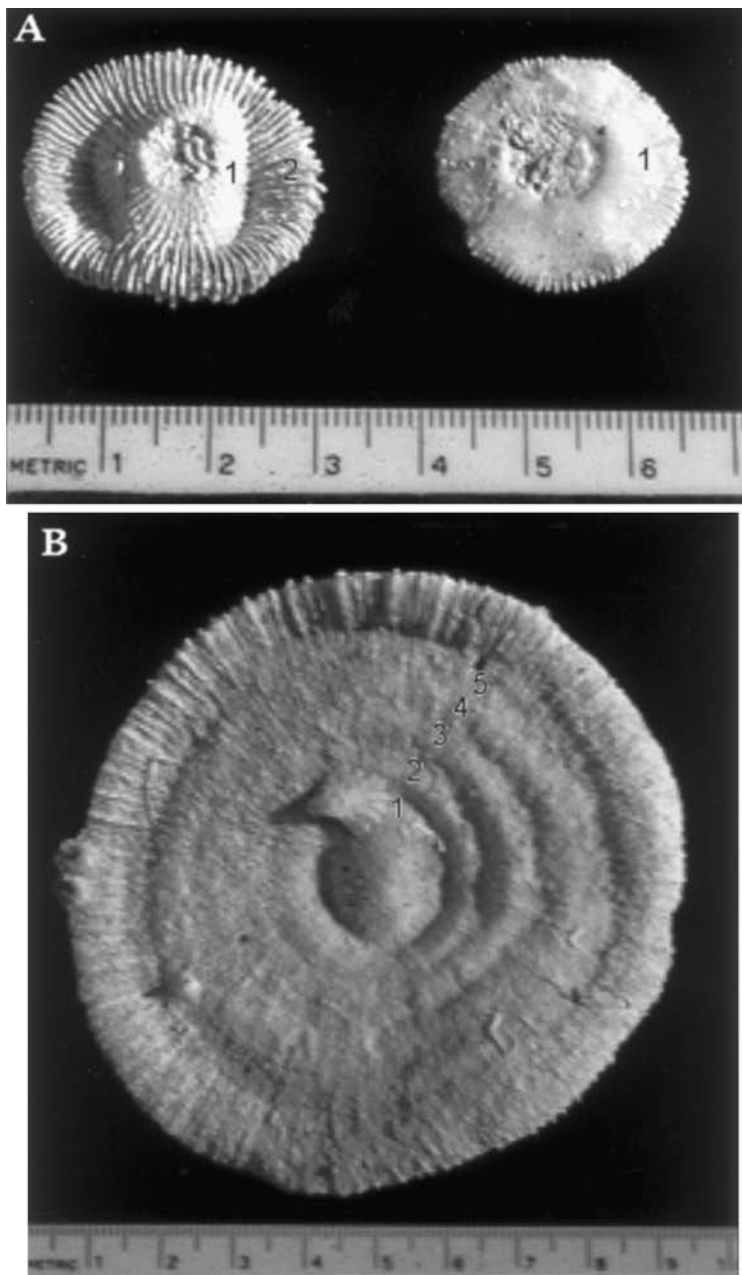


Fig. 1. Aboral view of skeletons of the mushroom coral *Fungia granulosa*, showing externally-visible growth rings. Each number denotes a ring, corresponding to a year of growth. Scale is in cm. (A) Coral on left is ~2 years old, coral on right is between 1 and 2 years old. (B) Coral is at least 7 years old. After about 6 years of growth, the rings became too close together to distinguish externally.

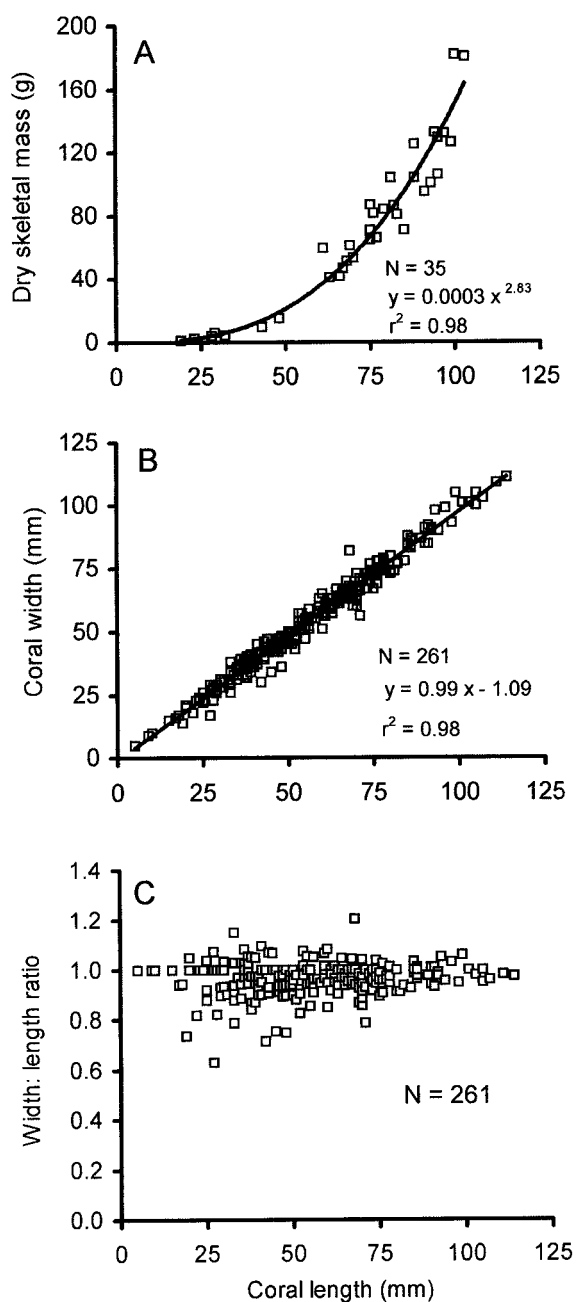


Fig. 2. Dependence of biometric parameters on individual length in the mushroom coral *Fungia granulosa*. (A) Dry skeletal mass. (B) Width. (C) Polyp shape (width:length ratio).

isometric. A width:length ratio of 0.96 ± 0.06 (mean \pm S.D., $N = 261$ polyps) indicated that the polyps were slightly oblong in shape (Fig. 2B and C).

The growth rate of individuals of *F. granulosa* decreased linearly with increasing coral size (Fig. 3). According to the von Bertalanffy growth function (see above), the rate of this decrease may be symbolized as a growth constant K , which is the slope of the linear regression line, with sign reversed. Thus, for the examined population of *F. granulosa*, the growth constant $K = 0.1095$ (Fig. 3). Maximum expected coral length in this population (L_∞) corresponded to the coral length at which growth rate became zero, or where the growth regression line intercepted the x -axis. Thus, for *F. granulosa* at Eilat, the maximum expected coral length $L_\infty = 118$ mm (Fig. 3).

From the above data, a lifetime growth curve for this population, according to the von Bertalanffy growth model, may be expressed by the following formula:

$$L_t = L_\infty(1 - e^{-Kt})$$

where L_t is the coral length at age t , L_∞ is the asymptotic length (maximum expected coral length), K is the growth constant, and t is the coral age.

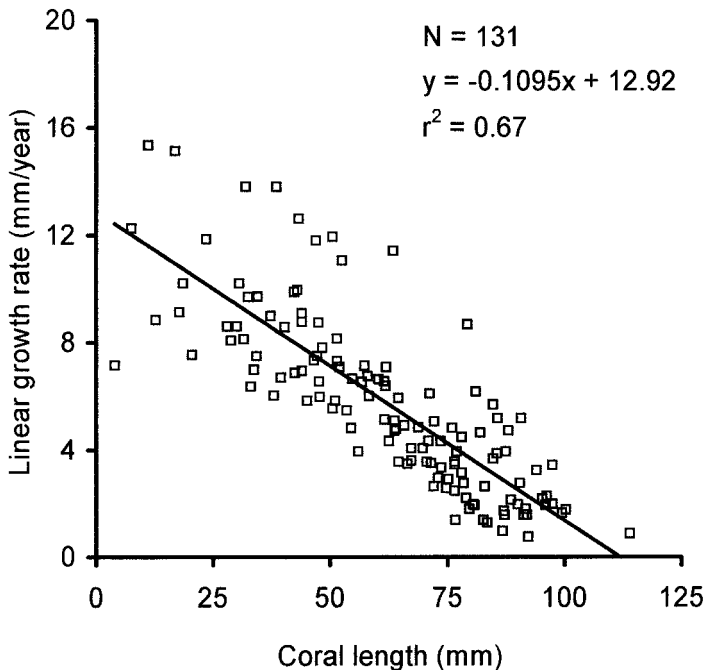


Fig. 3. Variation in linear growth rate among individuals of the mushroom coral *Fungia granulosa*. From in situ field measurements of individual corals during 0.5–2.5 years on a reef slope at Eilat, northern Red Sea. Note that linear growth rate decreases with coral size. The annual growth constant (K) is equal to the slope of the regression line, with sign reversed.

Using the values obtained above for K and L_{∞} , the growth curve for *F. granulosa* in Eilat was:

$$L_t \text{ (mm)} = 118(1 - e^{-0.1095t(\text{years})}).$$

According to this growth curve, individuals of *F. granulosa* reached maximal individual length at ~35 years of age (Fig. 4A). When young (0–5 years old), the corals grew relatively rapidly (mean \pm S.D. = 9.9 ± 1.7 mm year⁻¹), but as they aged their growth rate decreased, and by the time they were 30–35 years old, grew at imperceptible rates of only 0.4 ± 0.1 mm year⁻¹ (Fig. 4A). Over the entire period of active growth (0–35 years of age), growth rate was $\sim 3.4 \pm 3.3$ mm year⁻¹. The above growth curve was based on estimated growth for each size class, and thus individual growth varied somewhat around the curve (Fig. 3 and 4A). For young corals <7 years in age, the growth curve produced similar age–size relationships as those obtained from skeletal growth rings; after this age, growth was so slow that growth rings became externally indistinguishable and thus unusable (Figs. 1 and 4A).

The growth curve for changes in mass with age in *F. granulosa* had a sigmoidal shape (Fig. 4A), due to the exponential relationship between length and mass, in which body mass was very small when corals were young (Fig. 2A). For corals 0 to 35 years old, the mean growth rate of skeletal mass was 6.2 ± 3.3 g year⁻¹ (mean \pm S.D.).

The size-frequency of individuals observed in the field population, when converted to an age-frequency distribution using the above age–size relationships, revealed a population dominated by young, small individuals (Fig. 4B). More than 95% of the population was <15 years old (<95 mm in individual length), and the largest individual observed was estimated to be 31 years old (=114 mm length). The mean age of corals in this sample was 7 years old. During the first year of life, most individuals occurred in the attached phase, but this proportion decreased until, by the third year, most individuals became free-living, detached polyps (Fig. 4B). Relatively few individuals in the attached phase were found in the field population, but once they became free-living, young individuals were observed at high frequencies (Fig. 4B).

From the above age-frequency distribution, the Beverton Holt model (see above) estimated the instantaneous mortality rate of individuals at each age, expressed as a function of the natural logarithm of the decrease in individual frequency with age:

$$N_t = N_0 e^{-Zt}$$

where N_0 is the initial number of individuals at age zero (new recruits), N_t is the number of individuals remaining at age t , Z is the instantaneous rate of annual mortality and t is the coral age.

Upon fitting this expression to the field data on age frequencies, we obtained the following relationship:

$$N_{t(\text{years})} = 51.94e^{-0.17t(\text{years})}.$$

This function represented a best fit to the data in Fig. 4B, and yielded an exponential regression coefficient of $r^2 = 0.76$. The age classes of 0–2 years were excluded from this analysis (Fig. 4B), because they are known to be underrepresented in field samples of

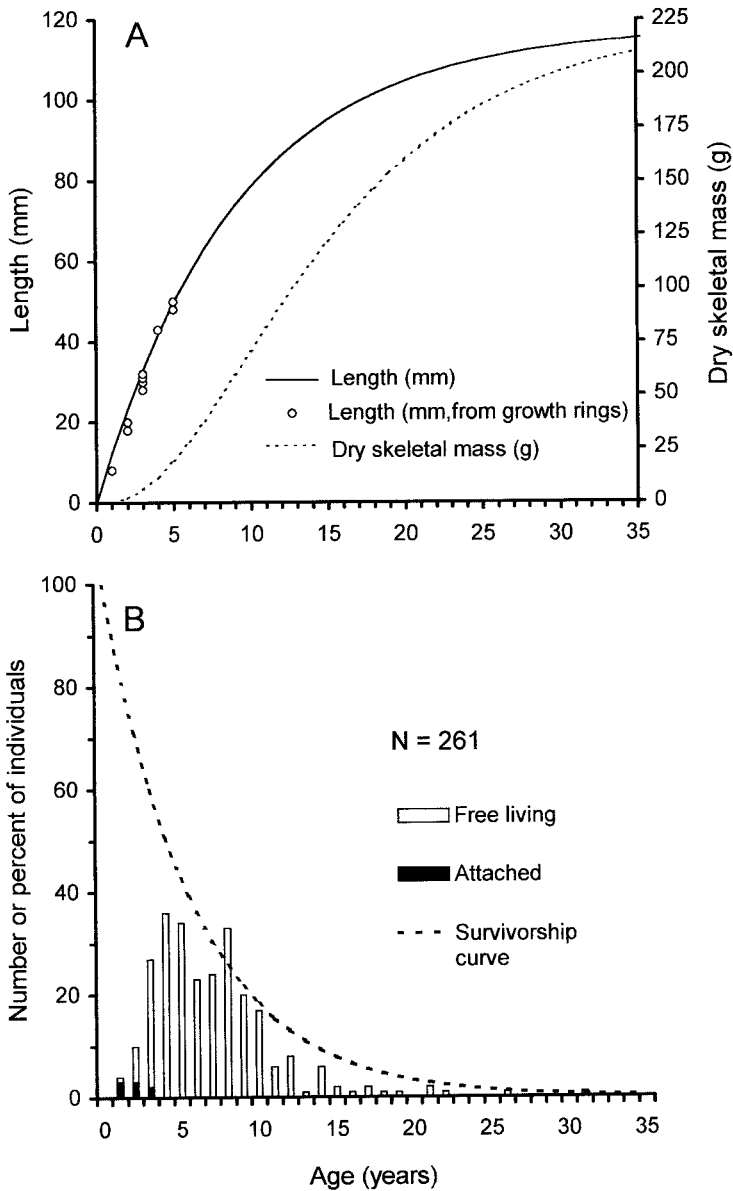


Fig. 4. Sizes and numbers of individuals of different ages in a population of the mushroom coral *Fungia granulosa*. (A) Age-specific growth curves obtained from application of a growth model to linear extension rates measured in the field, with comparative data from skeletal rings. (B) Age-frequency structure (bars, number of individuals) and survival curve (dotted line, percent of individuals) for corals on a reef slope at Eilat, northern Red Sea.

Table 1

Age, survival and yield of the mushroom coral *Fungia granulosa* on a reef slope at Eilat, northern Red Sea. Shown in bold are the age at sexual maturity (=6 years, calculated from Kramarsky-Winter and Loya, 1998), and the age at maximum yield (=9–10 years)

Age (years)	Length (mm)	Skeletal mass (g)	Survival	Yield (g/rec)
0	0	0.0	1.000	0.00
1	12	0.4	0.844	0.34
2	23	2.2	0.712	1.57
3	33	6.1	0.600	3.66
4	42	11.8	0.507	5.98
5	50	19.3	0.427	8.24
6	57	28.2	0.361	10.18
7	63	38.1	0.304	11.58
8	69	48.6	0.257	12.49
9	74	59.5	0.217	12.91
10	79	70.5	0.183	12.90
11	83	81.4	0.154	12.53
12	86	92.1	0.130	11.97
13	90	102.4	0.110	11.26
17	100	138.6	0.056	7.76
21	106	165.8	0.028	4.64
25	110	185.0	0.014	2.59
29	113	198.2	0.007	1.39
33	115	207.0	0.004	0.83

corals (Grigg, 1984; Babcock, 1991). Thus, the survival curve for members of this population, as given by the above function, estimated the mean age of individuals to be 6 years, and the oldest individual to be about 30 years old (Fig. 4B). Individuals had a high mortality rate when young, and the few surviving large, old individuals experienced low mortality (Fig. 4B).

The above data were used to calculate the yield, in terms of skeletal mass per recruit, of *F. granulosa* individuals at Eilat (Table 1). Cohort yield (=individual mass×percent survival) increased rapidly when the polyps were young, due to their rapid increases in size. Yield became maximal at age 9–10 years, after which losses due to mortality overtook gains due to individual growth. The age at maximum yield occurred 3–4 years after the polyps reached sexual maturity at 6 years of age (=60 mm length, Table 1). By the age of 33 years, <1% of polyps remained in the population.

4. Discussion

4.1. General

We show here that growth in the mushroom coral *Fungia granulosa* is size-dependent, with virtual cessation of growth after about 35 years of age. We also demonstrate that the mortality rate of these corals in a natural population decreases exponentially with coral

age, and thus that maximum biomass of the population is achieved by the time a cohort is about 9–10 years old. These data demonstrate that the sampled population is young and dynamic, and that there is a high turnover rate of these fungiid corals on Eilat reefs. Our results are the first attempt to model the life history and population dynamics of a mushroom coral, and have important implications for reef conservation management.

4.2. Coral shape and size parameters

Assessment of coral shape parameters in *F. granulosa* revealed that the corals have a slightly elongated discal shape (width:length ratio = 0.964), which they do not change as they grow (Fig. 2). An essential condition of the von Bertalanffy growth function employed here is that individual shape does not change with age, in other words, that mass is proportional to the cube of length throughout the lifespan, and thus that growth in mass is isometric (von Bertalanffy, 1938). Individuals of *F. granulosa* grow isometrically, in that mass is a cubed function of length, and the width:length ratio remains constant throughout life (Fig. 2). This condition occurs only in fungiid corals that retain a circular discal shape, and do not become elongated or bud polyp mouths along the disk's central axis, as occurs in the fungiid genera *Herpolitha* and *Ctenactis* (Hoeksema, 1989). Isometric growth in mass also has been demonstrated for the almost-circular solitary individuals of *Fungia actiniformis*, whose width:length ratio remains constant throughout life, at 0.927–0.942 depending upon locality (Abe, 1940). In contrast, the solitary polyps of *F. paumotensis* elongate as they grow, their width:length ratio decreasing from 0.810 to 0.639 as the individuals age (Bablet, 1985). Thus, due to less active skeletal secretion across the polyp's width over time, adult individuals of *F. paumotensis* have a smaller surface area compared to those of *F. granulosa* and *F. actiniformis* of equal length.

4.3. Growth rate and models

Many reef-building corals are known to grow indeterminately, and thus theoretically to have unlimited body size (reviewed in Hughes and Jackson, 1985; Bak and Meesters, 1998). However, the paradigm of unlimited growth in stony corals does not apply to all reef-building species. Despite their essentially 2-dimensional tissues and thus lack of surface area to volume constraints on growth, some corals are known to reduce their growth rate as they age. Scleractinian corals with size-dependent growth include some species that form branching colonies (*Pocillopora bulbosa* (Stephenson and Stephenson, 1933), *P. cespitosa* (Tamura and Hada, 1932), and *P. meandrina* (Grigg and Maragos, 1974)), massive colonies (*Goniastrea aspera* (Motoda, 1940; Sakai, 1998)), attached solitary polyps (*Balanophyllia elegans* and *Paracyathus stearnsii* (Gerrodette, 1979)) free-living colonies (*Manicina areolata* (Johnson, 1992)), and free-living solitary polyps (the mushroom corals *Ctenactis echinata* (Goffredo, 1995), *Diaseris distorta* (Yamashiro and Nishihira, 1998), *Fungia actiniformis* (Tamura and Hada, 1932), *F. fungites* (Stephenson and Stephenson, 1933), *F. granulosa* (present study, Figs. 3 and 4), and *F. paumotensis* (Bablet, 1985)). In free-living corals, which often colonise soft substratum, a genetic limitation on maximum size may represent an adaptation to avoid

sinking (Chadwick-Furman and Loya, 1992). Among attached corals, other constraints may influence maximal size, such as the biomechanics of a skeleton with highly branched architecture, or the physiology of a solitary polyp with a single mouth.

The pattern of size-dependent growth observed here in *F. granulosa* appears to fit the von Bertalanffy growth function (Figs. 3 and 4). The maximum individual length predicted by the model ($L_{\infty} = 118$ mm) is similar to that observed in the field population sampled at Eilat (maximum observed length is 114 mm for a coral 31 years of age, Fig. 4). In addition, the age–size curve derived from the model closely fits the age–size relationship obtained from analysis of annual skeletal growth rings in the corals, at least for young individuals (Fig. 4A). The external growth rings visible on the aboral skeleton of fungiid corals are a unique feature for the non-destructive aging of these corals, and also have been used to accurately age individuals of *F. actiniformis* (Abe, 1940). Our growth curves indicate that individuals of *F. granulosa* grow rapidly in length when young, increasing their mass more slowly, and reach a plateau for both mass and length sometime between 30 and 40 years of age, at which point they effectively stop growing (Fig. 4A).

Life history characters such as growth rate, maximum adult size and life expectancy vary widely between species of mushroom corals, and between populations within species (Table 2). According to our field data, members of three fungiid species examined in the northern Red Sea appear to take longer to reach maximum size (as described by the growth constant K) and to live longer than do members of the four species examined thus far in the tropical-equatorial Pacific (Table 2). Individual *F. actiniformis* that were investigated at a port entrance in Palau grew much more slowly than did all other fungiids studied in the tropical-equatorial Pacific (Table 2), possibly because they were exposed to anthropogenic stress. In contrast, growth rates of the fungiid coral *Diableris distorta* measured at Okinawa (sub-tropical Pacific) were relatively high, but were obtained under optimal laboratory conditions (Table 2) which may not reflect growth in the natural environment. In general, the values for growth rate, adult size, and life expectancy that we obtained here for *Fungia granulosa* were within the range of those known for other fungiids in habitats throughout the Indo-Pacific (Table 2).

4.4. Population dynamics

The size and age structure of the examined population showed an exponential decrease in the frequency of individuals with age (Fig. 4B). This structure indicates a population in steady state, in that no age cohorts were missing or over represented, as would be the case if a major disturbance event had recently altered recruitment patterns (Grigg, 1977, 1984; Santangelo et al., 1993). In contrast to this population on the reef slope, fungiid corals occurring on the shallow reef flat at Eilat are occasionally impacted by extreme low tide disturbances, and their population structure reflects a non-steady state (Loya, 1975). Eilat is located at the northern end of an enclosed sea, and thus corals on the reef slope occur in a relatively stable environment (Chadwick-Furman and Loya, 1992; Kramarsky-Winter and Loya, 1998), which may explain their steady state condition (Fig. 4B). Other coral populations known to occur in a steady state include

Table 2

Estimated maximum length (L_{∞} , mm), growth rate constant (K , annual), mean linear growth rate (M , mm year⁻¹) and life expectancy (E , years) of mushroom corals (Scleractinia: Fungiidae)

Species	Reference	Locality	Environment	Depth (m)	L_{∞}	K	M	E
<i>Ctenactis echinata</i>	Goffredo, 1995	Sharm el Sheikh (northern Red Sea)	Natural field	6–12	323	0.1086	9	34
<i>Diaseris distorta</i>	Yamashiro and Nishihira, 1998	Okinawa (subtropical Pacific)	Aquarium	–	19	0.3600	2	10
<i>Fungia actiniformis</i>	Tamura and Hada, 1932	Caroline Islands (tropical-equatorial Pacific)	Natural field	0–10	106	0.2199	6	17
	Abe, 1940	Palao (tropical-equatorial Pacific)	Port entrance	0–2	195	0.0839	4	44
<i>F. fungites</i>	Stephenson and Stephenson, 1933	Great Barrier Reef (tropical-equatorial Pacific)	Natural field	0–3	133	0.2150	8	17
	Goffredo, 1995	Sharm el Sheikh (northern Red Sea)	Natural field	6–11	107	0.0878	3	42
<i>F. granulosa</i>	Present study	Eilat (northern Red Sea)	Natural field	6	118	0.1095	4	35
<i>F. paumotensis</i>	Bablet, 1985	Mururoa, Tahiti (tropical-equatorial Pacific)	Natural field	10	147	0.4041	16	9

those of the stony reef-builder *Pocillopora verrucosa* (Grigg, 1984; Ross, 1984), the gorgonians *Muricea californica* (Grigg, 1977) and *Lophogorgia ceratophyta* (Mistri, 1995), and the commercially important precious corals *Corallium rubrum* (Santangelo et al., 1993), *C. secundum* and *Anthipathes dichotoma* (Grigg, 1984).

According to population dynamic models, the rate of instantaneous mortality (Z) equals the inverse of the mean age of the animals in a population, and hence is equal to their turnover rate, or annual production:biomass ratio (P/B) (Clasing et al., 1994). The turnover time for *F. granulosa* at Eilat is 5.88 years (calculated as the reciprocal of Z), indicating rapid turnover in this population of reef corals. Our estimates of mortality rate and life expectancy for *F. granulosa* appear to be reasonable, in that values derived from the survival curve closely reflect the field observations (Fig. 4B). Annual mortality rate and individual life expectancy are known to vary widely between the few species of anthozoans examined thus far (Table 3). In *F. granulosa*, values for both of these life history traits are within the range of those known for other stony reef corals (Table 3).

We observed relatively few 1–2-year-old individuals of *F. granulosa* in the field at Eilat (Fig. 4B). Two phenomena may explain this pattern. Firstly, newly settled individuals may be underrepresented because of the difficulty in locating them. Young, attached juveniles of fungiids and other reef corals may occur mainly in cryptic environments on the reef (reviewed in Chadwick-Furman and Loya (1992), Goffredo and Chadwick-Furman (2000)), and so the youngest age classes of corals are usually excluded from population dynamic analyses (Grigg, 1984; Babcock, 1991). In addition, fungiid corals have a life-history feature that further complicates the relationship between small and large individuals. When a young disk-shaped mushroom coral detaches from the reef, it leaves behind a stalked base that contains live tissue, and which may produce a small number of additional polyps (Hoeksema, 1989). Long-term field observations on the tagged stalks of fungiid corals at Eilat indicate that they may produce new free-living individuals at a rate of approximately one each year (mean \pm S.D. = 13.0 ± 5.5 months, range = 9–23 months, $N=10$ stalks; Chadwick-Furman, unpublished data). The height of the stalk indicates how many polyps were previously released, with each release represented by a ring on the stalk (Hoeksema, 1989; Yamashiro, 1992). A maximum of five rings were found on the stalked bases of *F. granulosa* observed at Eilat (mean \pm S.D. = 2.0 ± 1.4 rings, $N=7$ stalks), suggesting that only a few polyps are released by each stalk before it ceases to produce. Thus, a given number of attached stalks of *F. granulosa* potentially produces up to five times as many free-living disk-shaped polyps (Fig. 4B). In other fungiid species, a maximum of only three polyps have been observed to be released from each stalk (Yamashiro, 1992). Due to this asexual proliferation, the ages of individual fungiid corals, as estimated by growth functions or skeletal rings, are best thought of as age since detachment from the stalked anthocaulus phase. Recruitment to a population of free-living fungiids is actually a combination of larval settlement and the repeated production of individuals by attached stalks on the reef. This combination of sexual and asexual reproduction in mushroom corals leads to the formation of small clones of unconnected, dispersed individuals (Yamashiro, 1992). This life history feature need not invalidate the use of models to describe and manage populations of mushrooms corals, as long as standard definitions of coral age and recruitment are clearly understood to be modified or altered in members of

Table 3
Mortality rates (Z , annual) and life expectancies (E , years) known for anthozoans

Taxon	Reference	Locality	Depth (m)	Z	E
Gorgonacea					
<i>Muricea californica</i>	Grigg, 1977	La Jolla (southern California)	14–20	0.06	90
<i>M. fruticosa</i>	Grigg, 1977	La Jolla (southern California)	14–20	0.14	39
<i>Paramuricea clavata</i>	Mistri and Ceccherelli, 1994	Messina (Mediterranean)	30–38	0.12	46
<i>Leptogorgia hebes</i>	Mitchell et al., 1993	Northeastern Gulf of Mexico	22	1.14	6
	Mitchell et al., 1993	Northeastern Gulf of Mexico	27	0.23	25
<i>L. virgulata</i>	Mitchell et al., 1993	Northeastern Gulf of Mexico	1–1.5	0.54	11
<i>Lophogorgia ceratophyta</i>	Mistri, 1995	La Spezia Gulf (Mediterranean)	19–22	0.07	77
<i>Corallium rubrum</i>	Santangelo et al., 1993	Calafuria (Mediterranean)	20–45	0.56	11
<i>C. secundum</i>	Grigg, 1976	Makapuu (Hawaii)	350–475	0.07	77
Antipatharia					
<i>Antipathes dichotoma</i>	Grigg, 1976	Maui (Hawaii)	44–58	0.07	77
Scleractinia					
<i>Goniastrea aspera</i>	Babcock, 1991	Great Barrier Reef (Australia)	0–3	0.12	46
	Babcock, 1991	Great Barrier Reef (Australia)	0–3	0.16	35
<i>Platygyra sinensis</i>	Babcock, 1991	Great Barrier Reef (Australia)	0–3	0.09	60
<i>Pocillopora verrucosa</i>	Ross, 1984	Cebu (Philippines)	1–10	0.61	10
		(On a reef with a coral fishery)			
	Ross, 1984	Cebu (Philippines)	1–11	0.34	17
<i>Balanophyllia elegans</i>	Fadlallah, 1983	Pacific Grove (central California)	10–15	0.80	8
	Gerrodette, 1979	Pacific Grove (central California)	9	0.15	37
	Gerrodette, 1979	Pacific Grove (central California)	21	0.12	45
	Gerrodette, 1979	La Jolla (southern California)	19	0.11	50
	Gerrodette, 1979	Pt. Loma (southern California)	14	0.06	91
	Gerrodette, 1979	Pt. Loma (southern California)	18	0.07	79
<i>B. europaea</i>	Goffredo, 1999	Tyrrhenian Sea (Mediterranean)	1–13	1.17	6
<i>Paracyathus stearnsii</i>	Gerrodette, 1979	La Jolla (southern California)	19	0.05	99
	Gerrodette, 1979	La Jolla (southern California)	35	0.01	590
	Gerrodette, 1979	Pacific Grove (central California)	21	0.03	213
<i>Fungia granulosa</i>	Present study	Eilat (northern Red Sea)	6	0.17	33

this group. Finally, members of some fungiid coral species are known to proliferate extensively via active fragmentation of the free-living disc (reviewed by Yamashiro and Nishihira, 1998) or by the budding of polyps from the damaged or dying tissues of detached adults (Kramarsky-Winter and Loya, 1998). In species where these forms of reproduction dominate, different types of models need to be applied in order to understand processes of population turnover and structure.

4.5. Applications to coral reef management

Use of the Beverton Holt yield per recruit model to describe population dynamics in *F. granulosa* has important implications for stony coral fishery management. This model has been applied previously to manage stocks of precious corals in Hawaii (Grigg, 1984) and the Mediterranean (Caddy, 1993), and of reef-building stony corals in the Philippines (Ross, 1984). According to our estimates, the minimum size of *F. granulosa* individuals that can be fished without eventually decimating the local population (= size at maximum yield) is 74–79 mm in length, reached at ~9–10 years of age (Table 1). Polyps of *F. granulosa* at Eilat are known to reach sexual maturity at 55 mm in length (Kramarsky-Winter and Loya, 1998), corresponding to an age of about 6 years (Table 1). Thus, a minimum size limit of 74–79 mm would allow a 3–4 year buffer during which individuals could reproduce sexually before harvest. The growth model we employed here probably estimates accurately the age at sexual maturity, because it provides an appropriate description of prematurity growth (Day and Taylor, 1997), as corroborated by skeletal rings (Figs. 1 and 4).

According to our survival curve data, the percent of sexually mature individuals in this population is 43% (Table 1). In our field sample of the population, this value is slightly higher (57%), due to under representation of the 0–2 year age classes (Fig. 4B). The short time to maximum yield in *F. granulosa* (9–10 years, Table 1) is similar to that of the stony coral *Pocillopora verrucosa*, which reaches maximum yield at only 6 years of age (Grigg, 1984; Ross, 1984). In comparison, cohorts of antipatharians and gorgonians reach their maximum yield at much older ages of 28–40 years (Grigg, 1976, 1984; Caddy, 1993).

In Hawaii, the Beverton Holt model has been applied to sustainably manage the precious coral fishery for the production of jewelry and art objects (Grigg, 1984). Although this model likely will not be applied at Eilat, where coral harvest is prohibited, our work provides population dynamic information for a fungiid coral in the Red Sea, that may be compared with populations elsewhere. More widespread application of this type of model to fisheries of reef-building corals, especially in southeast Asia (Bentley, 1998), would reduce over-harvesting and the rapid depletion of stony coral populations in economies that depend upon this important natural resource.

Acknowledgements

We thank the staff of the Interuniversity Institute for Marine Science for their administrative and technical assistance, especially K. Tarnaruder for help with the

graphics. We are also grateful to Prof. F. Zaccanti of the University of Bologna for valuable advice on data elaboration and models. A. Balderman, S. Bensur, T. Feldstein, O. Langmead, E. Snider and D. Torovetzky assisted during the field work. This study was partially supported by an immigrant scientist fellowship from the Israeli Ministry of Science to N.E. Chadwick-Furman, funds from Scuba Schools International (Italy) to S. Goffredo, and funds to Y. Loya from the Porter Super-Center for Ecological and Environmental Studies, Tel Aviv University. [AU]

References

- Abe, N., 1940. Growth of *Fungia actiniformis* var. *palawensis* Doederlein and its environmental conditions. Palao Trop. Biol. Station Stud. 2, 105–145.
- Babcock, R.C., 1991. Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. Ecol. Monogr. 61, 225–244.
- Bablet, J.P., 1985. Report on the growth of a scleractinia (*Fungia paumotensis*). In: Proceedings 5th International Coral Reef Symposium, Tahiti, Vol. 4, pp. 361–365.
- Bak, R.P.M., Meesters, E.H., 1998. Coral population structure: the hidden information of colony size-frequency distributions. Mar. Ecol. Prog. Ser. 162, 301–306.
- Bentley, N., 1998. An overview of the exploitation, trade and management of corals in Indonesia. Traffic Bull. 17, 67–78.
- Caddy, J.F., 1993. Background concepts for a rotating harvesting strategy with particular reference to the Mediterranean red coral *Corallium rubrum*. Mar. Fish. Rev. 55, 10–18.
- Chadwick, N.E., Loya, Y., 1990. Regeneration after experimental breakage in the solitary reef coral *Fungia granulosa* Klunzinger, 1879. J. Exp. Mar. Biol. Ecol. 142, 221–234.
- Chadwick-Furman, N., Loya, Y., 1992. Migration, habitat use, and competition among mobile corals (Scleractinia: Fungiidae) in the Gulf of Eilat. Red Sea Mar. Biol. 114, 617–623.
- Clasing, E., Brey, T., Stead, R., Navarro, J., Asencio, G., 1994. Population dynamics of *Venus antiqua* (Bivalvia: Veneracea) in the Bahia de Yaldad, Isla de Chiloe, Southern Chile. J. Exp. Mar. Biol. Ecol. 177, 171–186.
- Connell, J.H., 1973. Population ecology of reef building corals. In: Jones, O.A., Endean, R. (Eds.), Biology and Geology of Coral Reefs, Vol. II, Academic Press, New York, pp. 271–324.
- Connell, J.H., Hughes, T.P., Wallace, C.C., 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol. Monogr. 67, 461–488.
- Day, T., Taylor, P.D., 1997. Von Bertalanffy growth equation should not be used to model age and size at maturity. Am. Nat. 149, 381–393.
- Fadlallah, Y.H., 1983. Population dynamics and life history of a solitary coral, *Balanophyllia elegans*, from Central California. Oecologia 58, 200–207.
- Gerrodette, T., 1979. Ecological Studies of Two Temperate Solitary Corals, University of California, San Diego, Ph.D. Thesis.
- Goffredo, S., 1995. Studio dell'accrescimento di *Ctenactis echinata* (Pallas, 1766) e di *Fungia fungites* (Linnaeus, 1758) (Madreporaria, Fungiidae) nella barriera corallina di Sharm el Sheikh, Sud Sinai, Egitto, University of Bologna, Bologna, Italy, M.Sc. Thesis; in Italian, with English summary.
- Goffredo, S., 1999. Population Dynamics and Reproductive Biology of the Solitary Coral *Balanophyllia europaea* (Anthozoa, Scleractinia) from the Northern Tyrrhenian Sea. In: University of Bologna, Bologna, Italy, Ph.D. Thesis; in Italian, with English summary.
- Goffredo, S., Chadwick-Furman, N.E., 2000. Abundance and distribution of mushroom corals (Scleractinia: Fungiidae) on a coral reef at Eilat, northern Red Sea. Bull. Mar. Sci. 66, 241–254.
- Grigg, R.W., 1974. Growth rings: annual periodicity in two gorgonian corals. Ecology 55, 876–881.
- Grigg, R.W., 1976. Fishery management of precious and stony corals in Hawaii. In: University of Hawaii Sea Grant Report #77-03, p. 48.

- Grigg, R.W., 1977. Population dynamics of two gorgonian corals. *Ecology* 58, 278–290.
- Grigg, R.W., 1984. Resource management of precious corals: a review and application to shallow water reef building corals. *P.S.Z.N.I. Mar. Ecol.* 5, 57–74.
- Grigg, R.W., Maragos, J.E., 1974. Recolonization of hermatypic corals on submerged lava flows in Hawaii. *Ecology* 55, 387–395.
- Hoeksema, B.W., 1989. Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). *Zool. Verh. Leiden* 254, 1–295.
- Hughes, T.P., 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. *Am. Nat.* 123, 778–795.
- Hughes, T.P., Jackson, J.B.C., 1985. Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.* 55, 141–166.
- Johnson, K.G., 1992. Population dynamics of a free-living coral: recruitment, growth and survivorship of *Manicina areolata* (Linnaeus) on the Caribbean coast of Panama. *J. Exp. Mar. Biol. Ecol.* 164, 171–191.
- Kramarsky-Winter, E., Loya, Y., 1998. Reproductive strategies of two fungiid corals from the northern Red Sea: environmental constraints? *Mar. Ecol. Prog. Ser.* 174, 175–182.
- Lewis, J.B., 1989. Spherical growth in the Caribbean coral *Siderastrea radians* (Pallas) and its survival in disturbed habitats. *Coral Reefs* 7, 161–167.
- Littler, M.M., Littler, D.S., Brooks, B.L., Koven, J.F., 1997. A unique coral reef formation discovered on the Great Astrolabe Reef, Fiji. *Coral Reefs* 16, 51–54.
- Loya, Y., 1975. Environmental predictability in relation to life histories of reef corals. In: *Proceedings Sixth Scientific Conference of the Israeli Ecological Society*, Jerusalem, pp. 215–223.
- Loya, Y., 1976a. Settlement, mortality and recruitment of a Red Sea scleractinian coral population. In: Mackie, G.O. (Ed.), *Coelenterate Ecology and Behavior*, Plenum Press, New York, pp. 89–100.
- Loya, Y., 1976b. The Red Sea coral *Stylophora pistillata* is an r strategist. *Nature* 259, 478–480.
- Loya, Y., 1990. Changes in a Red Sea coral community structure: a long-term case history study. In: Woodwell, G.M. (Ed.), *The Earth in Transition: Patterns and Processes of Biotic Impoverishment*, Cambridge University Press, Cambridge, pp. 369–384.
- Mistri, M., 1995. Population structure and secondary product of the Mediterranean octocoral *Lophogorgia ceratophyta* (L. 1758). *P.S.Z.N.I. Mar. Ecol.* 16, 181–188.
- Mistri, M., Ceccherelli, V.U., 1993. Growth of the Mediterranean gorgonian *Lophogorgia ceratophyta* (L., 1758). *P.S.Z.N.I. Mar. Ecol.* 14, 329–340.
- Mistri, M., Ceccherelli, V.U., 1994. Growth and secondary production of the Mediterranean gorgonian *Paramuricea clavata*. *Mar. Ecol. Prog. Ser.* 103, 291–296.
- Mitchell, N.D., Dardeau, M.R., Schroeder, W.W., 1993. Colony morphology, age structure, and relative growth of two gorgonian corals, *Leptogorgia hebes* (Verrill) and *Leptogorgia virgulata* (Lamarck), from the northern Gulf of Mexico. *Coral Reefs* 12, 65–70.
- Motoda, S., 1940. The environment and the life of massive reef coral, *Goniastrea aspera* Verrill, inhabiting the reef flat in Palao. *Palao Tropical Biological Station Studies* 2, 41–80.
- Ross, M.A., 1984. A quantitative study of the stony coral fishery in Cebu, Philippines. *P.S.Z.N.I. Mar. Ecol.* 5, 75–91.
- Sakai, K., 1998. Delayed maturation in the colonial coral *Goniastrea aspera* (Scleractinia): whole-colony mortality, colony growth and polyp egg production. *Res. Popul. Ecol. (Kyoto)* 40, 287–292.
- Santangelo, G.M., Abbiati, M., Caforio, G., 1993. Age structure and population dynamics in *Corallium rubrum* (L.). In: Cicogna, F., Cattaneo-Vietti, R. (Eds.), *Red Coral in the Mediterranean Sea: Art, History, and Science*, Min. Ris. Agr. Al. For, Rome, pp. 131–157.
- Shlesinger, Y., Loya, Y., 1991. Larval development and survivorship in the corals *Favia fava* and *Platygyra lamellina*. *Hydrobiologia* 216–217, 101–108.
- Stephenson, T.A., Stephenson, A., 1933. Growth and sexual reproduction in corals. *Great Barrier Reef Expedition 1928–29. Sci. Rep.* 3, 167–217.
- Stokes, M.D., 1996. Larval settlement, post-settlement growth and secondary production of the Florida lancelet (= amphioxus) *Branchiostoma floridae*. *Mar. Ecol. Prog. Ser.* 130, 71–84.
- Tamura, T., Hada, Y., 1932. Growth rate of reef building corals inhabiting in the South Sea Island. *Sci. Rep. Tohoku Imp. Univ., 4th Ser., Biology* 6, 433–455.

- von Bertalanffy, L., 1938. A quantitative theory of organic growth (Inquiries on growth laws. II). Hum. Biol. 10, 181–213.
- Yamashiro, H., 1992. Skeletal dissolution by scleractinian corals. In: Proceedings 7th International Coral Reef Symposium, Guam, Vol. 2, pp. 1142–1146.
- Yamashiro, H., Nishihira, M., 1998. Experimental study of growth and asexual reproduction in *Diaseis distorta* (Michelin, 1843), a free-living fungiid coral. J. Exp. Mar. Biol. Ecol. 225, 253–267.